VARIATION IN CONE MORPHOLOGY OF BALSAM FIR, ABIES BALSAMEA[1]

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Balsam fir, *Abies balsamea* (L.) Miller, is a widely distributed forest tree species in North America. The extent of its distribution is problematical in that Boivin (1959) has proposed the reclassification of the alpine fir of western United States and Canada, *A. lasiocarpa,* as a subspecies of balsam fir. Such reclassification would markedly extend the natural range and the amount of variation in taxonomic characteristics currently recognized within *A. balsamea.*

Considering only the more eastern taxon (Figure 1) as *A. balsamea* (L.) Miller, recognition of variation in the species has been largely restricted to observations on the relationship between the length of cone scales and the length of the bract that subtends each cone scale. Taxonomic identification of variation in balsam fir was proposed by Fernald (1909) with assignment of the varietal name *phanerolepis* to variants in which bracts were sufficiently long to be exposed in the mature cone (exserted). The variety *phanerolepis* has been shown to be most common in the Maritime Provinces of Canada, the St. Lawrence Valley, and at higher altitudes on mountains of the northeastern United States (Fernald, 1950; Myers and Bormann, 1963). The scale-bract relationship has been the chief characteristic used in maintaining Fernald's varietal distinction. Boivin (1959) noted the absence of discontinuities in the bract-length/cone scale length ratio in a sample of cones from Quebec but maintained the variety *phanerolepis* in his classification. Myers and Bormann (1963) reported altitudinal and longitudinal gradients in the scale/bract ratio and questioned the taxonomic validity of variety *phanerolepis.*

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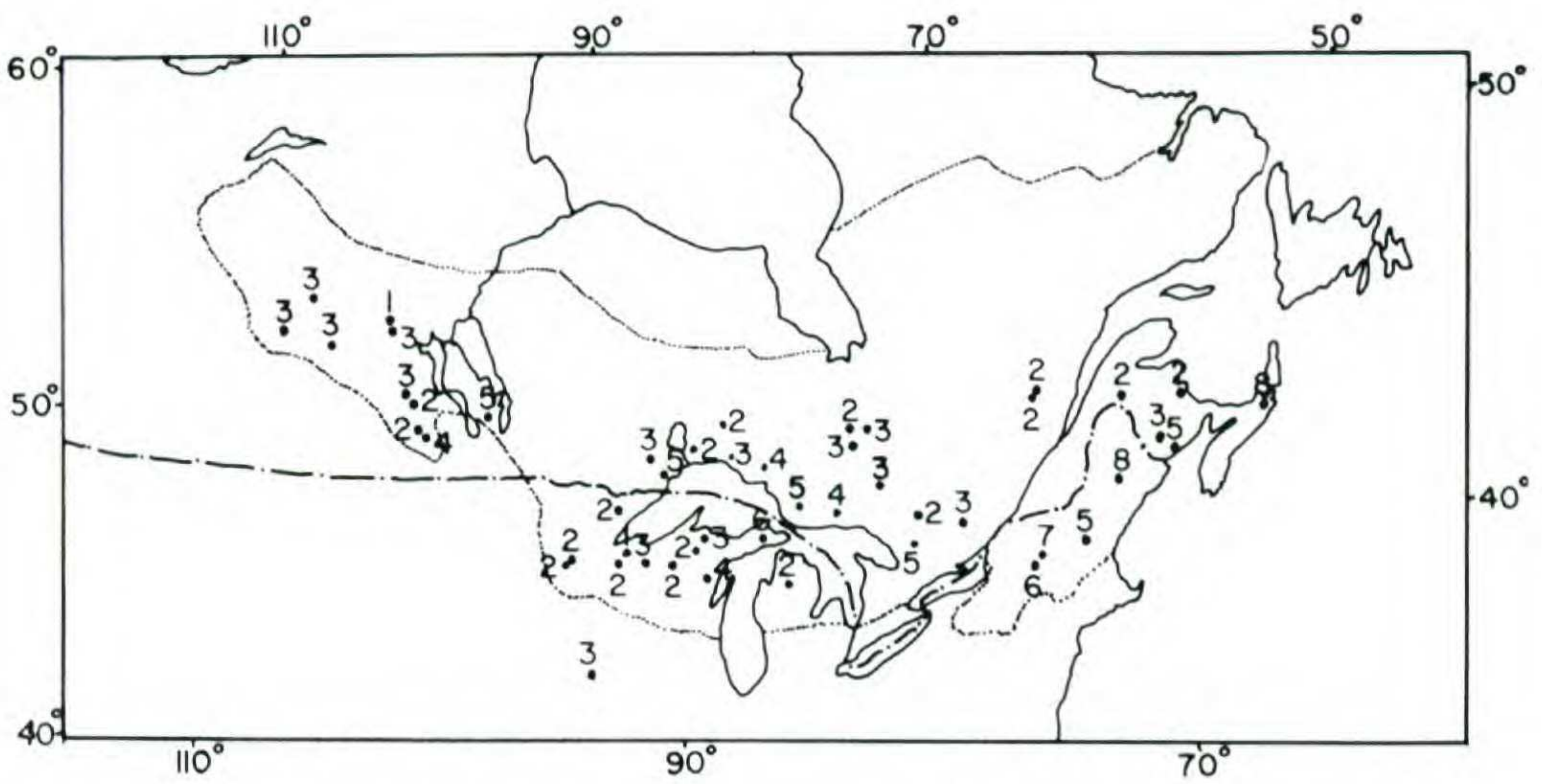

Figure 1. Natural range of balsam fir (. . . .), location of collections (.), and score of bract length/scale length ratios. Scores represent eight equal subdivisions of the array of ratios ranging from .44 to .80.

The study reported here represents a westward extension of the area sampled in earlier studies, a more intensive study of variation in cone morphology of balsam fir, and analyses of possible associations between variation in cone morphology and climatic variables. This study is a part of investigations of variation in balsam fir which include seed source or provenance tests currently in progress.

METHODS

In the period 1960 to 1966, seed collections of balsam fir were made by personnel of the University of Wisconsin and by cooperators in the United States and Canada. One hundred populations representing much of the readily accessible natural range were sampled. As an adjunct to the collection of cones for seed, intact cones from 49 populations (Figure 1) were preserved in formalin-acetic acid-alcohol solution. Ten of the cone collections were made in 1960 (northern Wisconsin and Michigan), 41 in 1962, one (Iowa) in 1964, and 5 in 1966. Elevations of the collections were generally within the range of 500 to 2000 feet although one New York collection came from an elevation of 3600 feet. Two cones, randomly chosen from each tree, were preserved and from two to ten trees were sampled at each location. Sample trees generally were scattered over an area of a few acres although some sample trees were separated by distances of up to three or four miles.

On each cone, cone width at the widest point and cone length were measured. Three cone scales were then removed from the middle of each cone for the measurements illustrated in Figure 2. These measurements were made using an ocular micrometer in a dissecting microscope.

Ten variables were studied. Measurements of length of cone, ovuliferous scale, seed wing, and bract were analysed

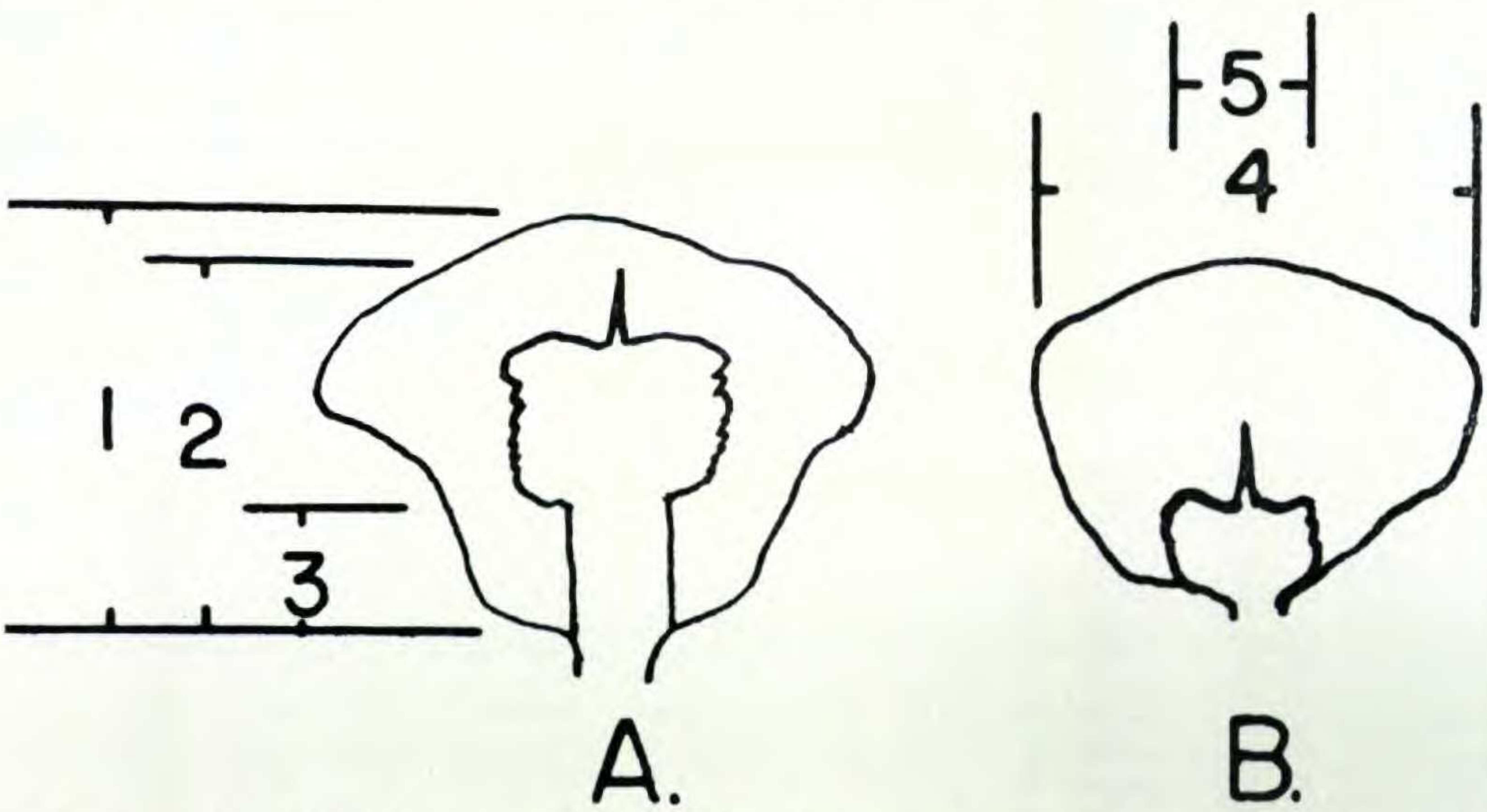

Figure 2. Sketches of abaxial view of ovuliferous scales and bracts. A. Maine collection, bract-scale ratio is .85. B. Western Ontario collection, bract-scale ratio is .50. Indicated measurements are 1. scale length, 2. bract length, 3. stalk length, 4. scale width, and 5. bract width.

directly. Due to the high frequency of zero, values for stalk length were transformed to $\sqrt{x + 0.5}$ before analysis. Ratios of length/width were calculated and analysed for cones, scales, wings, and bracts, along with the ratio bract length/scale length as a measure of bract exsertion.

Four sources of variation were hypothesized; variation associated with geographic location, with differences between trees in locations, with differences between cones within trees, and with differences among measurements within cones. Analyses of variance (Table II) were used to estimate whether each of the proposed sources of variation contributed significantly to the total variation. The relative contribution of each source was estimated by extension of the analysis of variance to computation of variance components.

Speculative associations between cone morphology and climatic variables were tested by linear correlation using mean values for each geographic location and for weather data from the station nearest to the collection location. Long-term averages were used; the period of recorded observations being 30 years for temperature and precipitation, and generally 10 years or more for frost-free period. Proximity of weather stations to cone collections was sometimes poor with distances being up to 50 miles in northern and western regions.

RESULTS

VARIATION IN CONE MORPHOLOGY

A sample of the arrays of average measurements for each location illustrate several points about variation in cone morphology in balsam fir (Table I). The arrays show a generally continuous pattern of variation with the exception of one New Brunswick collection in which length of the ovuliferous scale was significantly greater (99% probability) than in any other location. Although collections from the eastern portion of the sampled range were mostly among those with the longest cones, no clear geographic grouping was apparent for most of the characteristics measured.

Cone length was chosen as the variable with which to organize the sample of arrays in Table I. It was expected that development of cone parts, with the possible exception of bracts, would be strongly correlated with cone length so that the arrays for all characteristics might be similar. From Table I it is apparent that although longer cones generally had longer scales, seed wings, and bracts, substantial variation independent of cone length was present. For example, average cone length for the Maine collection was significantly longer than for either Wisconsin collection and yet no significant differences were apparent in scale or seed wing length for the three locations. Ratios of length/width showed less relation to cone size than length measurements, suggesting that differences in the shape of cone parts were not primarily functions of cone length.

The ratio of particular interest was bract length/scale length. For this ratio a geographic grouping of high values in the eastern portion of the range is apparent (Figure 1). The arrangement of scales in the fir cone is such that portions of the bract are generally visible when the bract length/scale length ratio exceeds 0.8 to 0.9. The highest average ratio for a location was 0.8 for the Nova Scotia collection. This value is appreciably less than the ratio of 0.9 suggested by Boivin (1959) or 1.0 suggested by Fernald (1909) for identifying the variety *phanerolepis*. However, the average ratio of measurements for one tree in the Nova Scotia collection exceeded 0.9 and the maximum value for a single measurement was 1.0. These observations emphasize the tree-to-tree variation as well as within cone variation for some cone characteristics.

COMPONENTS OF VARIATION

The analyses of variance indicated that locations, trees within locations, and cones within trees all contributed significantly (at 99% probability) to the observed variation in all measurements and ratios. The relative contributions of each source of variation are summarized in Table II.

Variation in cone length was associated approximately equally with differences between locations, between trees within locations and between cones within trees. For the other measurements, the predominant sources of variation were differences between geographic locations and between trees within locations. Variation associated with location was pronounced for bract and stalk length while tree-to-tree variation was predominant in length/width ratios with the exception of the ratio for bracts.

Variation associated with differences between cones from the same tree was relatively small in measurements of cone parts and in ratios. This suggests that except for measures of cone size, a small sample of cones from a given tree will accurately reflect the floral morphology of that tree.

Variation associated with samples from the same cone was either small or large depending on the variable considered. Restricting the sampling to the mid-portion of each cone unquestionably reduced sampling variation because ovuliferous scales at either end of the cone are smaller than in the middle. Bract length/scale length ratios also vary somewhat from base to tip of the cone. Variation within cones is thus probably greater for all characteristics measured than variation between cones from the same tree.

The predominance of geographic effects on variation in bract and stalk length suggests that bract development is of primary importance in relation to geographic distribution of balsam firs with different bract/scale ratios. During measurement of cone parts, it seemed that variation in stalk length might be contributing in a major way to variation in bract length. To test this speculation, the contributions of variation in stalk length and in blade length to variation in total bract length were estimated. Average values for geographic locations were used in multiple regression analysis. Contrary to impressions during measurement, the analysis revealed that variation in stalk length contributed only about 17% more than variation in blade length.

CORRELATION WITH CLIMATIC VARIABLES

The possible association of variation in cone morphology with certain climatic variables was tested by simple correlation. Frost-free period, mean annual temperature and precipitation, and mean monthly temperatures for May, June, and July were the climatic variables used. Table IV summarizes the statistically significant correlations and illustrates the association of bract development with climate. In view of the impossibility of obtaining weather data known to be representative of the collection location, the correlations must be interpreted with particular caution. Yet, the moderate correlation between bract characteristics and mean annual temperature and precipitation fits well with other analyses in which geographic location of the cone collection was shown to be the predominant source of variation in bract length.

DISCUSSION

Studies of variation in samples from native populations represent one type of approach to describing variation within species. These studies can complement experiments on comparative genetics and physiology conducted through the common-environment approach. Sampling in native populations commonly emphasizes structures which are less easily modified by environment so that the observed pattern of variation may more closely resemble patterns of genetic variation. Floral characters are generally less subject to environmental modification, perhaps as a result of differentiation and development of primordia over relatively short periods of time (Stebbins, 1950). Cones have been the structures of chief interest in studies of variation in balsam fir.

In the present study, samples from much of the readily accessible range of the species have shown generally continuous variation in measurements on cones and cone parts, as well as in measures of shape by length/width ratios. The continuity of variation, however, did not reflect a completely random pattern of geographic distribution. The more eastern collections were generally grouped near the top of some arrays, particularly those involving characteristics of the bract. The apparent association of variation in some cone characters with precipitation and temperature suggests that the grouping of eastern collections may be a reflection of climatic characteristics in the eastern portion of the range. It might be expected, therefore, that in other portions of the range, variation in local climates or years of unusually heavy rainfall at critical stages in cone initiation or development could produce similar variation.

On the other hand, the major contribution of trees within locations to total variation suggests that genetic differences or local environment associated with soil differences, crown position, or stand density could cause much of the observed variation. Fernald (1909), in proposing the variety *phan-*

erolepis, noted that trees bearing cones with exserted bracts were growing intermingled among trees of the species type at Percé Mountain on the Gaspé Peninsula. Myers and Bormann (1963) similarly found trees characterized by cone scale/bract ratios ranging from variety *phanerolepis* to variety *balsamea* within the St. Lawrence Valley, Gaspé Peninsula, and Maine, although from their data it is not clear whether the whole range of variation was present in any one small group of trees.

Possible genetic control of variation in the bract/scale ratio is suggested by comparison of the cones of variety *phanerolepis* with *A. fraseri*, a species currently restricted to high elevations in the Southern Appalachian Mountains. Cones of *A. fraseri* are characterised by exserted and strongly reflexed bracts wherever the species is grown. In *A. balsamea*, altitudinal clines for the cone scale/bract ratio have been demonstrated, with exserted bracts being predominant at the highest elevations (Myers and Bormann, 1963). In *A. fraseri*, gene fixation for bract development may have resulted from restriction of the species to high elevations following a xerothermic or hypsithermal period (Mark, 1958). In *A. balsamea* the high elevation gene pool remains connected to lowland populations. The relative contributions of environment and genetic differentiation to variation in cone morphology of *A. balsamea* eventually should be estimable in the common-environment experiments now in progress.

The influence of geographical location of cone collection was most evident in the variation in bract length. Although the correlations in Table IV must be viewed with particular caution, the apparent moderate association of bract length with mean annual temperature and mean annual precipitation coincide with the indicated influence of geographic location. Variation in the developmental pattern of bracts may thus be the basis for the variety *phanerolepis*.

Fernald (1950) defined a variety as "a strongly fixed variation of a species with the essential reproductive parts unchanged but showing somewhat constant departures in size of parts, shape of leaves, or modification of the less fundamental parts of the flower, etc. and occupying a somewhat segregated geographic area". If distinct discontinuity in the pattern of variation is not a prerequisite for varietal classification, Fernald's definition seems most questionable on the point of "a strongly fixed variation . . . showing somewhat constant departures . . .". The separation of genetic and environmental influences on bract development will be necessary to establish how strongly fixed and how constant is variation in bract development. Assignment of a bract length/cone scale length ratio of about 0.9, or, more simply, assigning trees bearing cones with exserted bracts to variety *phanerolepis*, will result in a geographic subdivision of the species range. Within that subdivision the frequency of trees classified as the variety *phanerolepis* will vary continuously along altitudinal and geographic gradients and perhaps from year to year. Varietal classification here serves merely to recognize an arbitrary, though visually prominent, point on a scale of continuous variation.

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Table I. Sample of arrays of mean value for geographic locations.

Geographic Location		Lengths (mm) Cone	Scale	Seed Wing	Bract	Stalk	Ratios Length/Width Cone	Scale	Seed Wing	Bract	Bract Length/ Scale Length
New Brunswick	45°58′N, 66°22′W	68.1	16.4	15.9	8.5	2.1	3.0	.87	2.3	1.4	.57
Maine	44°45′ , 68°37′	63.2	11.6	13.8	9.1	2.5	3.1	.71	2.3	1.7	.79
New Brunswick	45°35′ , 66°19′	62.4	13.2	15.2	8.5	2.1	2.7	.73	2.2	1.5	.65
New York	44°19′ , 73°55′	59.0	11.6	14.0	9.0	3.6	2.6	.69	2.2	1.5	.78
Ontario	46°25′ , 79°10′	57.2	11.7	13.9	5.9	0.8	3.2	.76	2.2	1.2	.51
New York	43°45′ , 74°07′	56.6	11.8	14.2	8.2	2.3	2.8	.71	2.1	1.5	.70
Overall Mean		51.9	11.1	13.0	6.3	0.8	2.8	.75	2.2	1.3	.57
Ontario	49°10′ , 80°15′	45.7	9.4	11.5	5.0	0.7	2.9	.68	2.1	1.2	.54
Nova Scotia	46°23′ , 60°40′	44.8	8.1	9.9	6.6	1.8	2.4	.56	2.0	1.0	.80
Wisconsin	45°58′ , 90°07′	44.7	9.5	11.8	5.2	0.7	2.6	.73	2.2	1.2	.56
Wisconsin	46°02′ , 89°32′	42.0	10.3	12.1	5.4	0.8	2.6	.76	2.2	1.2	.52
Saskatchewan	53°55′ ,101°15′	41.6	9.8	11.6	5.3	0.7	2.4	.75	2.1	1.2	.55
New Brunswick	47°05′ , 65°28′	35.0	9.6	11.2	4.8	0.7	2.0	.67	2.1	1.0	.51
Approximate significant difference with 99% probability (from Duncan, 1955 with p = 25)		11.0	2.6	2.3	1.2	0.2	0.5	0.14	0.3	0.2	0.14

Table II. Summary of analyses of variance.

A. General form of analysis

Source of Variation	Degrees of Freedom	Expected Mean Squares
Geographic Location	48	$\sigma_m^2 + C_1\sigma_c^2 + C_2\sigma_t^2 + C_3\sigma_l^2$
Trees in Location	256	$\sigma_m^2 + C_1\sigma_c^2 + C_2\sigma_t^2$
Cones in Trees	299	$\sigma_m^2 + C_1\sigma_c^2$
Measurements in Cones	1206	σ_m^2

σ_m^2, σ_c^2, σ_t^2, σ_l^2 = components of variance associated with measurements, cones, trees, and locations respectively.

C_1 = Mean number of measurements per cone = 3.0
C_2 = Mean number of measurements per tree = 5.9
C_3 = Mean number of measurements per location = 36.8

B. Components of variance expressed as a percentage of total variance.

Source of Variation	Length					Length/Width Ratio				
	Cone	Scale	Seed Wing	Bract	Stalk	Cone	Scale	Wing	Bract	Bract L/ Stalk L
Geographic Location	31	36	35	58	47	21	14	14	39	38
Trees in Location	39	49	42	26	28	49	40	44	36	36
Cones in Trees	30	11	17	8	9	30	5	13	8	10
Measurement in Cones	—	4	6	7	15	—	40	28	16	16

Table III. Correlation of cone measurements with measures of climate.

Cone Measurement	Annual Precipitation	Annual Temperature
Scale Length (L)	—.01	—.01
Length/Width (L/W)	.38**	—.20
Bract L	.35**	.29*
L/W	.12	.42**
Stalk L	.61**	.46**
Bract L/Scale L	.43**	.35**

* correlation coefficient differs significantly from 0 with 95% probability

** correlation coefficient differs significantly from 0 with 99% probability

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